

Description of a New Pleurobranch
(Opisthobranchia: Notaspidea) from Antarctic Waters,
with a Review of Notaspideans from
Southern Polar Seas

by

RICHARD C. WILLAN

Department of Zoology, University of Queensland, St. Lucia,
Brisbane, Queensland 4067, Australia

AND

HANS BERTSCH¹

Department of Biological Sciences, National University,
San Diego, California, U.S.A.

Abstract. This paper describes the first side-gilled sea slug from Antarctica—*Bathyberthella antarctica*, spec. nov. It is unusually large for a member of its group and distinguished externally by its remarkably large foot and dark gray, blotched markings. Anatomically it compares closely to the abyssal *B. zelandiae* Willan, the only other species of the previously monotypic genus. The chief differences relate to body size, proportions of the foot, shell, and reproductive system. *Bathyberthella antarctica* has secondarily lost its penial gland. Three other species of the Pleurobranchidae, all belonging to the genus *Berthella*, occur in Subantarctic waters: *B. patagonica* (Orbigny), *B. platei* (Bergh), and *B. medietas* Burn.

INTRODUCTION

WITHIN THE OPISTHOBRANCH order Notaspidea, the greatest diversity of genera and species occurs in tropical seas and very few taxa exist in polar waters—indeed the genera *Tylodina*, *Tylodinella*, *Umbraculum*, *Pleurobranchus*, *Berthellina*, *Pleurehdera*, *Euselenops*, *Pleurobranchaea*, and *Pleurobranchella* are completely absent. Hitherto only three species of *Berthella* (*B. patagonica*, *B. platei*, and *B. medietas*) have been reported authentically from Subantarctic waters. Two species of *Pleurobranchaea* (one

unidentified and *P. maculata*) have distributions whose southern limits impinge upon Subantarctic waters. This present work adds one additional genus, *Bathyberthella*, to the list of southern polar taxa, and the new species, *B. antarctica*, has the most southerly distribution of any recorded notaspidean species. Actually it is the only species of the order that could be termed truly Antarctic. Because of this species' novel locality and phylogenetic importance, we wish to describe it in a separate paper and, in doing so, review the known notaspideans from adjacent Subantarctic waters.

Fifteen specimens of this new notaspidean were located among a collection of opisthobranchs procured under the auspices of the United States Antarctic Research Program (USARP). The entire marine faunal collection, which was

¹ Mailing address: 6056 Beeman Avenue, No. Hollywood, CA 91606, U.S.A.

dredged by the Antarctic Research vessels *Hero*, *Islas Orcada*, and *Eltanin* between the years 1962 and 1983, has been curated by the Smithsonian Oceanographic Sorting Center of the United States National Museum. The 456 specimens constituting the opisthobranch collection represent six major taxonomic groups: cephalaspideans, notaspideans, gnathodorids, cryptobranch dorids, dendro-notaceans, and aeolids (BERTSCH, 1985).

TAXONOMY

Genus *Bathyberthella* Willan

Type species, by original designation, *Bathyberthella zelandiae* Willan, 1983.

Bathyberthella antarctica Willan & Bertsch, spec. nov.

Figures 1a, 2-17

Description: Only preserved specimens were available for study. They ranged between 65 and 93 mm so, assuming a reduction in size of about one-quarter due to contraction on death, we believe the maximum extended crawling length for an adult would be approximately 120 mm. The mantle is ovate or elliptical in shape and slightly convex dorsally; the anterior margin is truncate and straight across; the two sides are parallel; the posterior margin is broadly rounded. The mantle is free from the underlying foot all round and much smaller than the foot, particularly posteriorly. This important character is illustrated diagrammatically in Figure 2. The mantle's surface is smooth, somewhat puckered and wrinkled posteriorly and laterally (possibly through contraction on death), but not pustulose. The foot is very large, thick, and spongy, and from above its edges are visible all round in all our specimens. Like the mantle, the upper surface of the foot is puckered and wrinkled posterior to the mantle, but it is not in the least pustulose. The sole of the foot has a very large, circular, thickened pedal gland posteriorly; its borders are not sharply marked off from the surrounding tissue on the tail's ventral surface. The front edge of the foot bears an extensive, semicircular mucous-gland groove dorsally. The point of fusion of the moderately short, widely diverging rhinophores is visible in front of the mantle in some of our specimens, but this is probably not the situation in life. The trapezoidal oral veil is as broad as the mantle; its anterior margin, which is almost straight across, is neither notched nor papillate; the longitudinally grooved sides extend, as tentacular extensions, a short distance anterolaterally. The gill is prominent, although its rear end does not extend to level with the hind end of the mantle. Its rachis is relatively narrow and entirely smooth, there being 17-21 (mean = 19.9) pinnae on (the upper side of) the rachis. The gill is free for about one-half its length, and the anus opens on the upper side of the gill at the hind end of the basement membrane.

The body is uniformly creamish gray in color with the

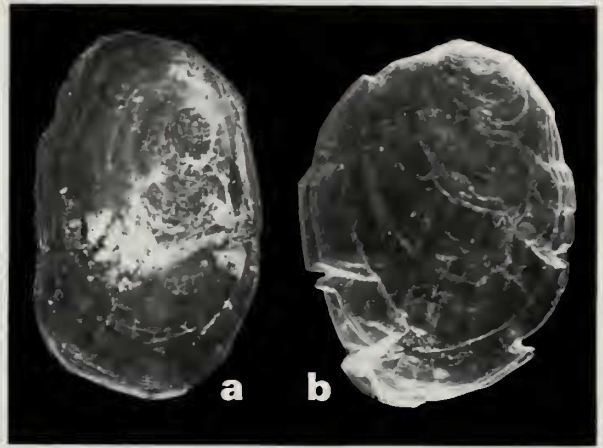


Figure 1

External view of shells of paratypes of *Bathyberthella* species. a, *B. antarctica*; length 63 mm \times width 39 mm. Specimen from 360 to 480 m, west of South Sandwich Islands, Scotia Sea, Antarctica, 30 May 1975. Preserved length 70 mm; b, *B. zelandiae*; length 23 mm \times width 18 mm. Specimen from 1676 m, northern side of Bounty Trough, New Zealand, 26 Oct. 1979. Preserved length 30 mm.

upper surface of the foot being paler than the mantle. The mantle itself is covered with extensive areas of dark pigment that are distinguishable as irregular blotches centrally and become confluent marginally. This darker pigment is not easily rubbed off. No specific markings are recognizable on the sides of the body, rhinophores, oral veil, or gill.

A shell (Figure 1a) was present beneath the mantle in all the specimens examined. It is large (e.g., 63 \times 39 mm in a specimen of 70 mm preserved length). The shell roofs the entire visceral cavity. There are no muscles attached to it and neither is it connected to the body wall or underlying integument. The shell is cuticular, thin, and fragile, and little more than a flexible membrane. It is easily deformed in any direction. All the shells possessed some vestigial calcification, merely a patch of thin white flakes, near the center a little to the right of the midline. The shape is oval to elongate with the greatest width nearer the anterior end than at the center; the anterior margin and posterior flange are both broadly rounded; and the lateral margins are slightly wavy and diverging. The protoconch is situated toward the posterior left corner, but not at the margin (i.e., it is subterminal) and there is an extensive posterior flange to the right of, and behind, it. The shell itself is virtually flat with concentric growth lines constituting the only sculpture. It shows localized crumpling caused by compression of the overlying mantle during fixation. It is shining, hyaline centrally, and faintly golden toward the margins.

The heart, which lies transversely, is located beneath

Table 1

Radular data for *Bathyerbthella antarctica*.

Specimen no.	No. rows	Formula	Preserved length (mm)
1	86	250.0.250	71
2	71	207.0.207	70

the shell's anterior margin a short distance behind the base of the rhinophores. The spherical, thick-walled ventricle is in the midline, and the conical, thin-walled auricle is situated immediately to its right.

The proboscis was everted in several specimens and this cylindrical, muscular introvert was moderately long, being about equal to the pharyngeal bulb in length. The pharyngeal bulb (Figure 3) has a sharp, oblique ridge on either side, and the single, tubular, dorsal accessory gland enters in the midline anteriorly at the front of the pharyngeal bulb. This gland is remarkably long (measuring about 250 mm when fully unravelled), with thinner walls and a greater diameter (approximately 1 mm) than the salivary glands. It is packed initially on the floor of the visceral cavity beneath the digestive gland on the right side, and then is further stacked at the top left corner. At no point along its length does it branch. The two extrinsic pharyngeal-bulb retractor muscles originate as one from the roof of the visceral cavity in the midline at the center of the body.

Radulae from two specimens were examined. Their formulae, together with the preserved length of each animal, are given in Table 1.

All the teeth are rather large and of simple form. Each consists of an erect, tall, parallel-sided blade that tapers gradually to a slightly recurved, sharp-pointed apex. The inner laterals (Figures 4a, b, 10) are relatively short (with a mean vertical height of 228.6 μm) and relatively broad; often the middle region of the outer face of the blade has one or two undulations (Figure 4b); the base is enlarged and triangular. The middle and outer laterals (Figures 4c, d, 11, 13, 14) are proportionately longer and narrower (with a mean vertical height of 292.9 μm). The outermost lateral teeth (Figures 4e, 12) are smallest, broader, and more curved than the inner or middle laterals, and none of the outermost laterals is reduced or peglike.

The two jaws (Figure 5) that line the pharyngeal bulb are large, elongate, and rather thin. The maximum length of a jaw, when flattened on a slide, is 14 mm and this corresponds to a width (measured between the parallel sides of the jaw, not at the anterior margin) of 6 mm. Each jaw is parallel-sided, with the anterior end much expanded and truncate where it curves back to join the labial cuticle. The jaws are composed of numerous, crowded mandibular elements that are irregularly grouped into wide, longitudinal rows with bare strips between them.

The mandibular elements themselves (Figures 6, 15-17) are narrow and elongate, and there is no indication of lateral processes on the sides of any of them (*i.e.*, the elements are not cruciform). At the surface of the jaw, the elements bear 1, 2, or 3 (rarely 4 or 5), sharp, conical cusps; all are well cuticularized. Rarely, subdenticles (*i.e.*, subsidiary points) are present on the sides of a few of the cusps (Figure 17). Generally, one stronger cusp is situated in advance of the others, but rarely all are in a line and each is of equal strength to all the others. These cusps project on the jaw's surface in wavy, frequently discontinuous, transversely oblique rows, and they are sometimes disorganized. The number of cusps on any one particular element seems to have no relationship with the numbers possessed by the element next to it.

The genital organs emerge, in preserved specimens, from a relatively large swelling and from this projects a high, raised ring of skin that forms a continuous circle around the everted genitalia.

The reproductive system of a mature individual occupies the bulk of the space within the visceral cavity. The ovotestis, which lies above and obscures the digestive gland, takes up the whole rear half of the visceral cavity. The anterior genital complex occupies the right front section. Three organs of the anterior genital complex are immediately visible from above: a bulky mucous gland at the back, a muscular vagina sandwiched in the middle, and the prostate gland at the front. The hermaphrodite duct passes, as a tubular ampulla, between the ovotestis and anterior genital complex dorsally close to the right body wall. The ampulla maintains its diameter throughout its considerable length and only constricts where it enters the anterior genital complex from the left side immediately behind the bursa copulatrix. The hermaphrodite duct runs, as a slender tube, through the middle of the genital complex; it gives off a short side branch (the proximal vas deferens), and then swells slightly before entering the nidamental glands.

The proximal vas deferens enlarges almost immediately to an enormous prostatic section (Figure 7). This section is uniformly glandular throughout its entire length, folded back upon itself, compressed, and closely applied to the ventral (*i.e.*, inner) surface of the bursa copulatrix. Ultimately, it narrows to a tightly coiled distal vas deferens which, without any appreciable change in diameter or presence of penial gland, eventually passes into the penis within a globular and muscular penial sheath. The penis is conical, elongate, and smooth, and it narrows evenly to an acutely pointed tip. Its interior possesses the vas deferens and numerous retractor muscles (Figure 8).

Immediately behind the penis is the vagina. This muscular canal, which tapers gradually along its length, leads straight to a large, spherical bursa copulatrix. Another duct of a slightly smaller diameter (the uterine duct) leads away from the base of the bursa, and a short distance along its length (approximately 8 mm) is a separate canal

to the receptaculum seminis. This is a small, fingerlike organ of uniform diameter that lies beside the bursa and next to the nidamental glands; it never reaches the surface of the genital mass. After that, the uterine duct continues via a great many sinuous loops (that are narrower than the section between the bursa and receptaculum) to enter the nidamental glandular complex at almost exactly the same point the hermaphrodite duct terminates.

The nidamental glands are enormous in a sexually mature animal. Two regions are discernible; a thin-walled, hollow mucous gland, whose walls are regularly pleated, that occupies the entire posterior face and a more solid area (consisting of possibly more than one gland) of closely packed, solid tubules. This is probably the albumen gland. These glands are not shown in Figure 9 because their gelatinous nature rendered the drawing of an exact outline impossible. Figure 9 represents a diagrammatic view of the structure of the reproductive organs in which omission of the nidamental glands could give the unintentional impression of a diallic condition. This is not the arrangement, as there are three quite separate canals (*i.e.*, vas deferens, oviduct, and uterine duct) within the pallial gonoduct.

Material examined: Holotype: 85 mm long (*i.e.*, length from anterior edge of oral veil to tip of tail) \times 54 mm wide (*i.e.*, maximum mantle width); 360–486 m depth, 56°40.6'S, 27°00.8'W, west of South Sandwich Islands, Scotia Sea, R/V *Islas Orcada* (cruise 575; station no. 62), 30 May 1975. United States National Museum of Natural History, Reg. No. USNM 859009.

Paratypes: Specimens collected with the holotype at station no. 62, undissected specimens dispersed as follows: 2 specimens, 93 mm long \times 59 mm wide and 78 mm long \times 50 mm wide, United States National Museum of Natural History, Reg. No. USNM 859010; 2 specimens, 74 mm long \times 47 mm wide and 54 mm long \times 32 mm wide, Los Angeles County Museum of Natural History, Reg. No. 2120.

Two specimens, 128–165 m depth, 63°50'S, 62°35'W, west of Graham Land, Antarctica, South Pacific Ocean, R/V *Eltanin* (cruise 6; station no. 439), 9 January 1963, both undissected, dispersed as follows: 1 specimen, 88 mm long \times 52 mm wide, California Academy of Sciences, Reg. No. CASIZ 057393; 1 specimen, 78 mm long \times 55 mm wide, Australian Museum, Sydney, Reg. No. C145497.

Remarks: Several of the characters of *Bathyberthella antarctica* merit comment. First of all is the size attained by adults. Although we have not seen a live specimen, we estimate the extended length of an adult would be approximately 120 mm. This size makes *B. antarctica* much larger than its single congener, *B. zelandiae* Willan, or any member of the three most closely related pleurobranch genera, *Berthella*, *Berthellina*, and *Pleurehdera*. In fact, it means *B. antarctica* falls within the size range of

species of *Pleurobranchus* (which attain between 60 and 300 mm crawling length as adults) and thus rekindles the old question of the natural subgroups of pleurobranchine pleurobranchs. (The debate, and resulting conflicting classifications of ODHNER [1926] and BURN [1962] were summarized by WILLAN [1983].) However, the large size of *B. antarctica* poses no real challenge to the now accepted scheme of Burn, because it is the only character *B. antarctica* shares with *Pleurobranchus* species. None of the other apomorphies of *Pleurobranchus* (*i.e.*, tuberculate mantle, mid-anterior mantle cleft, or flaps surrounding the genital aperture) is possessed by *Bathyberthella antarctica*. Therefore, this new species actually reinforces Burn's scheme, later supported by WILLAN (1983), that the Pleurobranchinae is divided naturally into two subgroups. Each should be ranked as a tribe. One tribe, Berthellini Burn, 1962, consists of "smaller" species with a non-tuberculate, non-emarginate mantle, and (usually) smooth gill rachis, and the other, Pleurobranchini Menke, 1828, consists of "larger" species with tuberculate, emarginate mantle, and pustulose gill rachis. Further evidence in support of these groupings has recently come from investigations of sperm ultrastructure (HEALY & WILLAN, 1984). *Bathyberthella antarctica* is the largest member of the former tribe. It exhibits gigantism, a common phenomenon among Antarctic biota (CALMAN & GORDON, 1933; PECKHAM, 1964; HARTMAN, 1966; WOHLSCHLAG, 1968; KOLTUN, 1970).

In pleurobranchs, the relative proportions of the mantle and foot change depending on the state of activity of the specimen. When one is crawling actively, the tail of the foot usually extends behind the mantle and at rest the foot tucks up beneath the mantle. The very large foot of *Bathyberthella antarctica* is surely an exception and, in life, it must extend beyond the mantle at all times. In one of our preserved specimens, the foot exceeded the mantle by 20 mm posteriorly. Possibly the substratum on which *B. antarctica* lives has necessitated this enlargement. Could it be that the foot now prevents this relatively large pleurobranch from floundering when it is crawling over fine muds?

One of the specimens collected in 1963 (C145497) has several forked pinnae on the upper side of the rachis near the end of the gill. The bifurcation commences high up near the point of origin from the rachis. We have never observed any bifurcation of pinnae like this previously in the Notaspidea. We are confident this configuration is the result of a mutation of the particular individual and not an aberration resulting from a previous injury or artifact of collection.

As is typical for the genus, *Bathyberthella antarctica* has a large number of teeth within radular rows but there is little differentiation (of size or shape) of teeth within the row.

The reproductive system is peculiar for the enormous development and bulk of the ovotestis, occupying as it does

Table 2
Comparison of character states between the two species of *Bathyberthella*.

Character	<i>B. antarctica</i> , spec. nov.	<i>B. zelandiae</i>
Maximum size (extended crawling length)	120 mm	40 mm
Color of mantle in life	Creamish gray with extensive areas of dark pigment, as blotches, centrally and more or less continuous marginally	Uniform translucent cream marked with small, vague white flecks and speckles; yellow spots occasionally present
Position of protoconch on shell	Subterminal (Figure 1a)	Terminal (Figure 1b)
Mean number of rows of teeth for adult	78.5	62.2
Mean number of teeth per row for adult	228.5	217
Penial gland	Absent	Present
Retractor muscle attached to vagina	Absent	Present

the entire back half of the visceral cavity. This increased gonad area could indicate extremely high fecundity. In addition to the magnitude of the ovotestis, the nidamental glands are also disproportionately large. The most important specific character as regards the reproductive system is the absence of a penial (sometimes referred to as accessory prostate) gland. This gland is present in *Bathyberthella zelandiae* and every species belonging to the three most closely related genera (*Berthella*, *Berthellina*, and *Pleurehdera*) that has been examined anatomically. We conclude the absence of the penial gland in *B. antarctica* is the result of loss. One can speculate that a section of the considerably enlarged prostate gland has taken over the function of the penial gland.

The discovery of a second species of a previously monotypic genus is always a special event for a systematist because of the foresight involved in erecting such a new taxon in the first place. Thus, the discovery of *Bathyberthella antarctica* is both gratifying and remarkable, and made all the more so by the significant place presently occupied by *Bathyberthella* within the family Pleurobranchidae (WILLAN, 1983). Willan initially suggested that this genus possessed characters linking the two subfamilies (Pleurobranchinae and Pleurobranchaeinae) of the Pleurobranchidae, but it is now apparent that *Bathyberthella* belongs in the Pleurobranchinae. However, we maintain strongly that the two higher taxa are subfamilies and not families as some taxonomists continue to do (e.g., EV. MARCUS & GOSLINER, 1984). Characters apparently possessed jointly by *Bathyberthella* and members of the Pleurobranchaeinae (specifically regarding the mandibular elements on the jaws) must now be reinterpreted in some way other than owing to retention of the plesiomorphic condition.

Bathyberthella antarctica and *B. zelandiae* both possess (1) a smooth mantle and gill rachis, (2) a very large, flexible, cuticular shell, (3) numerous, narrow, erect, smooth radular teeth, (4) oval or elliptical mandibular elements that lack lateral processes and have an irregu-

larly denticulate anterior margin, (5) a triaulic reproductive system with vas deferens extensively dilated into a prostate gland, (6) a smooth penis, (7) a globular penial sheath, and (8) two allosperm receptacles. The particular character states for the shell, radula, and mandibular elements are synapomorphies that together justify the continued recognition of *Bathyberthella* as a valid genus.

On the other hand, the two species possess several dissimilar characters that irrefutably separate them. Those characters existing in clearly different states are summarized in Table 2. Chief among them are the last two that involve the reproductive system, the more notable being the lack of a penial gland in *Bathyberthella antarctica*. In that species, the prostate gland is relatively more extensive, the uterine duct is longer, and the receptaculum seminis does not come directly off the base of the bursa copulatrix but instead it begins a short distance (approximately 8 mm) down the bursal stalk. Apart from those to do with the reproductive system, two other characters are evident, both involving relative proportions of the body. One concerns the mantle and foot; in *B. antarctica* the mantle is much smaller than the foot all round, whereas in *B. zelandiae* the mantle is only a little shorter than the foot at the rear. The other character is the length of the extended proboscis; this structure is shorter in *B. antarctica*, being able to evert for about 10 mm in an adult, whereas in *B. zelandiae* it can be protruded for a distance equal to half the body length.

REVIEW

For over a century and a half, international expeditions have been sampling southern polar (i.e., Antarctic and Subantarctic) oceans and so the benthic fauna is reasonably well known today. The mollusks have arguably received the most attention and, among them, the opisthobranchs have been amply covered. Usually opisthobranchs are neglected on non-specific sampling voyages because of difficulties inherent in preserving them. An extensive lit-

erature search has been made to review what is known about Antarctic and Subantarctic notaspidean opisthobranchs and the results are presented here.

We preface this review by explaining that we follow DELL's (1962) subdivision of southern polar waters into three more or less concentric zones (High Antarctic, Antarctic, and Subantarctic) and five biogeographic regions (Continental Antarctic, Magellanic, Tristan da Cunha, Kerguelenian, and South Georgian District). Dell argues strongly and cogently against the need for, or validity of, marine faunal provinces (*e.g.*, DELL, 1962, 1972). We find much to support in his plea for distributional data instead of more marine provinces.

Knowledge of the southern polar opisthobranch fauna has been gained from the following expeditions and investigators (*i.e.*, only those researchers who actually reported on opisthobranchs): A. d'Orbigny's explorations in southern America, for which he documented the opisthobranchs himself (ORBIGNY, 1835-1846); the *Challenger* expedition (1873-1876) documented by WATSON (1886); L. Plate's expedition to South America documented by BERGH (1898); The Belgian Antarctic Expedition (1897-1899) documented by PELSENEER (1903); a Falkland Islands collection documented by ELIOT (1907a); the Swedish South Polar Expedition (1901-1904) documented by STREBEL (1908) and ODHNER (1926); the German South Polar Expedition (1901-1903) documented by THIELE (1912); the Scottish National Antarctic Expedition (1901-1904) documented by ELIOT (1905, 1907b); the French Antarctic Expeditions (1903-1905 and 1908-1910) both documented by VAYSSIÈRE (1906, 1917 respectively); the British Antarctic (*Terra Nova*) Expedition (1910-1913) documented by EALES (1923) and ODHNER (1934); the Australasian Antarctic Expedition (1911-1914) documented by HEDLEY (1916); Mortensen's Pacific Expedition (1914-1916) documented by ODHNER (1924); the Norwegian Antarctic Expeditions (1927, 1928 *et seq.*) documented by ODHNER (1944); the Discovery Investigations (1925-1939) documented by POWELL (1951); the British-Australian-New Zealand Antarctic Research Expedition (1929-1931) documented by POWELL (1957, 1958) with summaries and extensions to Subantarctic islands by POWELL (1955, 1960, 1965); the Lund University Chile Expedition (1957) documented by ER. MARCUS (1959); the 12th (1961-1963) and 15th (1964-1965) French Antarctic Expeditions documented by VICENTE & ARNAUD (1974); a Davis Sea collection documented by MINICHEV (1972).

The combined total of notaspideans from all of these investigations on opisthobranchs is a mere two species, both belonging to the genus *Berthella*. Each will be dealt with separately below. Two species of *Pleurobranchaea* from opposite extremes of the southern Pacific have distributions that could possibly impinge, at their southern limits, upon Subantarctic waters. *Pleurobranchaea maculata* (Quoy & Gaimard) is known from the southern New

Zealand mainland and southern Tasmania so, like *Berthella medietas* mentioned below, *P. maculata* may well occur at the Subantarctic islands to the south of New Zealand or Australia. Specimens of another species of *Pleurobranchaea* have been taken on two occasions near the Juan Fernandez Islands off the central Chilean coast (BERGH, 1898; ODHNER, 1922). This species may possibly have a Magellanic distribution with its range extending, in Subantarctic waters, down the west coast of South America. However, because of the uncertainty of existing records (all being based on juvenile specimens) and the impreciseness of BERGH's (1898) account, no one can be sure of the identity of this particular southeastern Pacific *Pleurobranchaea* species. BERGH (1898) called it *P. maculata* (Quoy & Gaimard) probably because that name was the only one established for any Pacific species (then known) belonging to *Pleurobranchaea*. VAYSSIÈRE (1901: 51) and EV. MARCUS & GOSLINER (1984) refuted Bergh's identification. Clearly no advance can be made until a thorough redescription of adults of this species is published.

Berthella patagonica (Orbigny, 1840)

Synonymy

Pleurobranchus patagonicus ORBIGNY, 1840 (date from RUSSELL, 1971): 203-205, pl. 17, figs. 4, 5; PILSBRY, 1896:200, 201, pl. 74, figs. 92, 93; BERGH, 1898:496-499, pl. 28, fig. 26, pl. 29, figs. 10-16.

Bouvieria patagonia (Orbigny): VAYSSIÈRE, 1898:289-291; CARCELLES & WILLIAMSON, 1951:312; ODHNER, 1926: 22.

Berthella patagonia (Orbigny): EV. MARCUS, 1984:50, figs. 2, 3.

The type locality for this pleurobranch is Ensenada de Ros on the southeastern coast of Argentina (41°S; *i.e.*, in the Magellanic Region). ORBIGNY's (1840) original description merely sketched the external features of this species, and it is apparent from his text (in particular the reference to the moundlike genital swelling and chalky nature of the shell) as well as from the illustration (especially the everted penis) that the account was prepared from preserved material. VAYSSIÈRE (1898) added nothing more when he wrote his comprehensive monograph on the Pleurobranchidae, but he did transfer the species to his new genus *Bouvieria*. BERGH (1898) had access to four specimens from Quiriquina in southern Chile and his account supplied many essential anatomical details. Because this species has apparently not been collected or reported on subsequently, our knowledge of its anatomy rests solely on the words of Bergh. This species undoubtedly belongs in the genus *Berthella* Blainville because of its small size, smooth and non-emarginate mantle, relatively large and rectangular shell, simple and curved radular teeth, and cruciform mandibular elements with denticulate blades. The color in life is, according to Orbigny, yellowish am-

ber: or translucent white with delicate yellowish tinges according to Bergh (*i.e.*, as reported in Plate's field notes). Unfortunately the two descriptions provide few significant characters that we can use to distinguish *Berthella patagonica* unambiguously from the thirteen other similar-looking, small pleurobranch species that occur elsewhere in the world, *i.e.*, *Berthella plumula* (Montagu), *B. aurantiaca* (Risso), *B. stellata* (Risso), *B. sideralis* (Lovén), *B. agassizii* (MacFarland), *B. strongi* (MacFarland), *B. tupala* Er. Marcus, *B. tamiu* Ev. Marcus, *B. americana* (Verrill), *B. platei* (Bergh), *B. pellucida* (Pease), *B. serenitas* (Burn), and *B. medietas* Burn.

Because *Berthella patagonica* was collected intertidally by Orbigny and Plate, it should be recollected without great difficulty. Hopefully a critical comparison will then be undertaken.

Berthella platei (Bergh, 1898)

Synonymy

- Pleurobranchus platei* BERGH, 1898:494-496, pl. 11, figs. 28-38; VAYSSIÈRE, 1901:77.
Bouvieria platei (Bergh): ODHNER, 1926:22, 24, pl. 1, figs. 6, 7; CARCELLES & WILLIAMSON, 1951:312.
Berthella platei (Bergh): ER. MARCUS, 1959:24-27, figs. 34-38.

The holotype was dredged in 18-34 m near Calbuco in southern Chile. ODHNER (1926) recorded a second specimen taken in 137-150 m on the Burdwood Bank west of Tierra del Fuego. Later ER. MARCUS (1959) provided further comparative data on 12 individuals that had been collected between 70 and 300 m off southern Chile. *Berthella platei* thus occurs in Subantarctic waters within the Magellanic Region.

The accounts of Bergh, Odhner, and Er. Marcus have provided a firm set of diagnostic characters by which *Berthella platei* can be defined. *Berthella platei* is, in life, pale and translucent pink with reddish-brown tinges on the mantle margin, oral veil, and rhinophores. Its large, circular, calcareous shell entirely roofs the visceral cavity. Its radula consists of simple, curved teeth and the cruciform mandibular elements possess three or four (either strong or weak) denticles on both sides of the blade. (Note, however, that BERTSCH [1975] AND WILLAN [1984] have shown that great intraspecific variability can exist in pleurobranchs' mandibular elements.) *Berthella platei* is unusual in that its anus opens above the anterior third of the gill basement membrane, the state also found in *B. medietas*. This character alone should provide a ready distinction between Magellanic pleurobranchs, even if only preserved specimens are available.

Berthella medietas Burn, 1962

Synonymy

- Pleurobranchus aurantiacus* Risso: BERGH, 1900:210-211, pl. 20, figs. 34-38 (non *Pleurobranchus aurantiacus* Risso, 1818).

- Bouvieria (Pleurobranchus) aurantiaca* (Risso): ODHNER, 1924: 51; POWELL, 1939:217, no. 1232 (non *Pleurobranchus aurantiacus* Risso, 1818).
Bouvieria aurantiaca (Risso): POWELL, 1955:118 (non *Pleurobranchus aurantiacus* Risso, 1818).
Pleurobranchus punctatus Quoy & Gaimard: BURN, 1957: 15 (non *Pleurobranchus punctatus* Quoy & Gaimard, 1832).
Berthella medietas BURN, 1962:135-137, 142, 146, pl. 1, fig. 3, pl. 2, figs. 7, 8, text figs. 1C, 2C (erroneously spelled *mediatas* on p. 142); MACPHERSON & GABRIEL, 1962: 252; BURN, 1966:271, no. 26 (erroneously spelled *mediatas*); 1969:80, no. 15 (erroneously spelled *mediata*); WILLAN, 1983:243-248, figs. 8, 32-44; 1984:43; WILLAN & MORTON, 1984:57; BURN in Phillips, 1984:71 (all erroneously spelled *mediatas*).

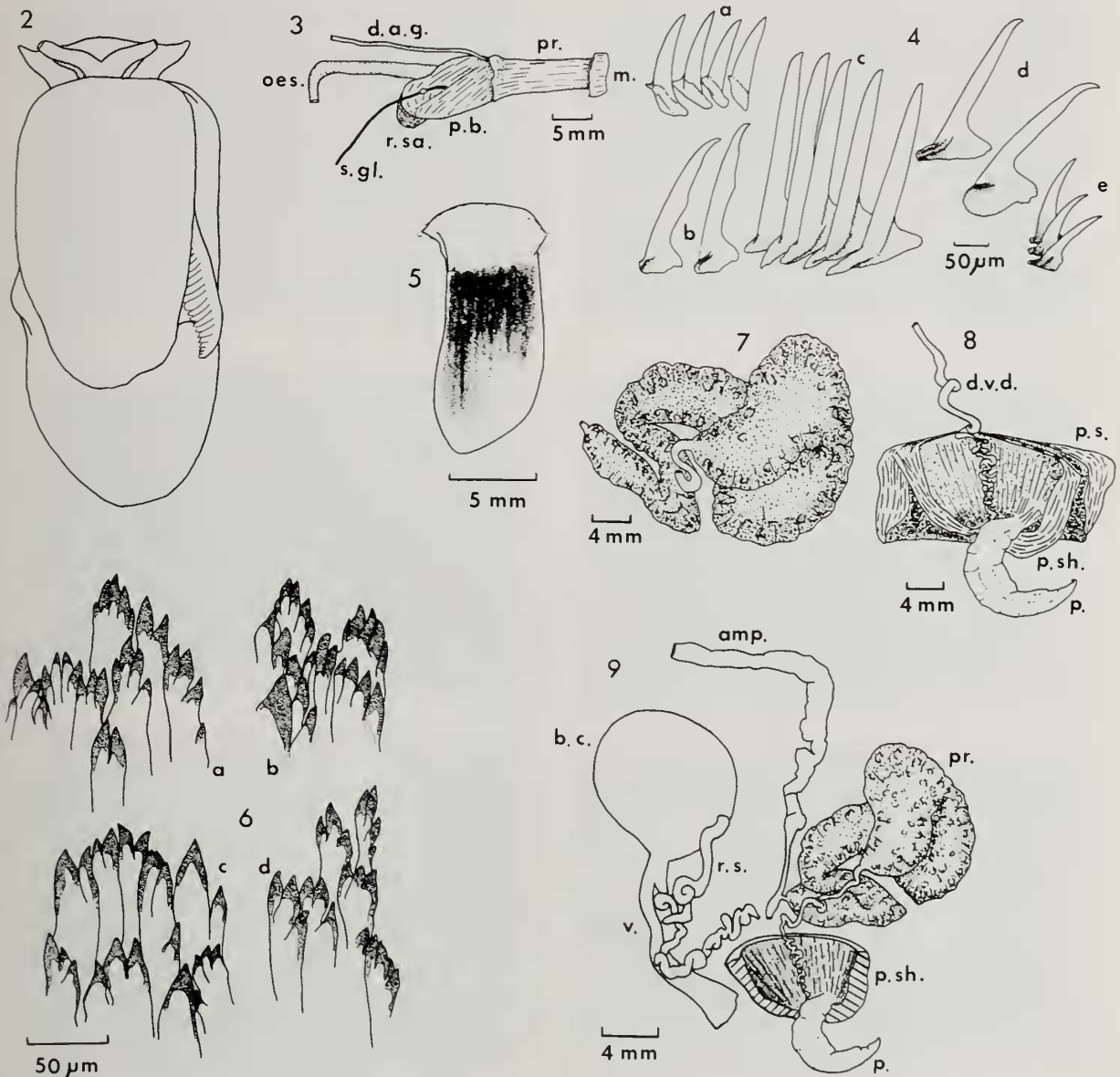
Burn (*in litt.*, 28 September 1985) states that a hitherto unnoticed error occurs in the spelling of the specific name for this species at the head of the original description (BURN, 1962:142, line 7). The correct spelling is *medietas*—Latin, feminine, meaning "the middle, midst, that which is in the middle." "The specific name is given because of the median position of the anus along the gill membrane" is the explanation for the specific name originally given by BURN (1962:143). Elsewhere in Burn's paper, the specific name occurs five times (pp. 135-137, 146) and is spelled correctly each time. Under the I.C.Z.N. (1985 edition), Article 32 (c) (ii), the specific name must be corrected to *medietas*.

Berthella medietas was first described from the central Victorian coastline of Australia (BURN, 1962) which is well north of the Subantarctic zone, and BURN in Phillips (1984) subsequently recorded it from South Australia and Tasmania. In the meantime, WILLAN (1983) recognized it from both main islands of New Zealand as well as Stewart Island and the Chathams. Furthermore, Willan identified ODHNER's (1924) species from Masked Island, Auckland Islands, which Odhner had wrongly called "*Bouvieria aurantiaca* (Risso)," as belonging to this species. At 50°30'S, the Auckland Islands lie on the northern boundary of the Subantarctic zone, so this species is admissible in this present review.

The distinctive characters of *Berthella medietas* are its pale, brownish-orange mantle which has a highly glandular (*i.e.*, porous) texture, deeply sinuous anterior margin to the oral veil, anus opening above the anterior third of the gill's basement membrane, large and rectangular shell with a flange on the columellar side, simple and hook-shaped teeth that show differentiation in size and curvature across rows, cruciform mandibular elements with (usually) strong denticles on the blades, possession of a penial gland, vas deferens lacking an enlarged prostatic section, and two allosperm receptacles of which the receptaculum seminis is distinctly club-shaped.

ACKNOWLEDGMENTS

We thank Dr. Gordon Hendler (currently of the Los Angeles County Museum of Natural History) and Mrs. Bet-



Explanation of Figures 2 to 9

Figures 2 to 9. Anatomy of *Bathyberthella antarctica*.

Figure 2. Dorsal view of adult depicting supposed appearance in life.

Figure 3. Right profile of foregut (extrinsic muscles not shown). Abbreviations: d.a.g., dorsal accessory gland; m., mouth; oes., oesophagus; p.b., pharyngeal bulb; pr., proboscis; r.sa., radular sac; s.gl., salivary gland.

Figure 4. Radular teeth: a, group of four inner (tooth on right is innermost) laterals from row three; b, isolated inner laterals; c, group of five middle laterals from center of radular row; d, isolated outer laterals; e, group of three outermost laterals.

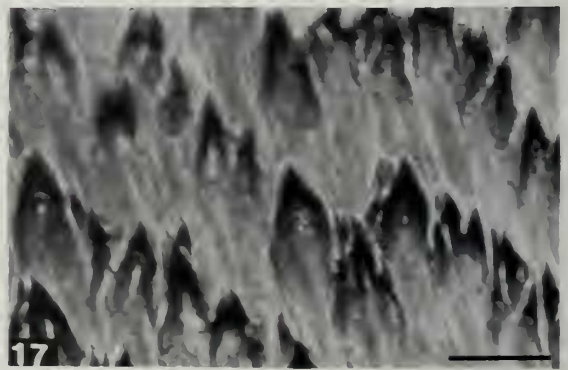
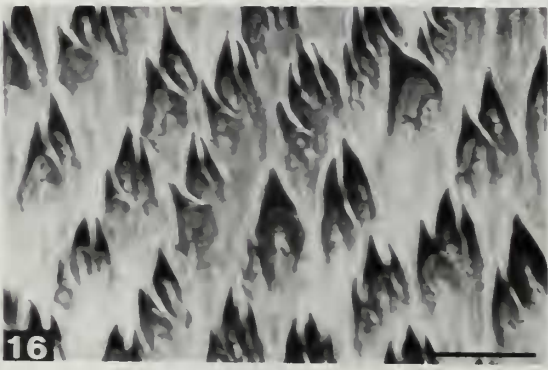
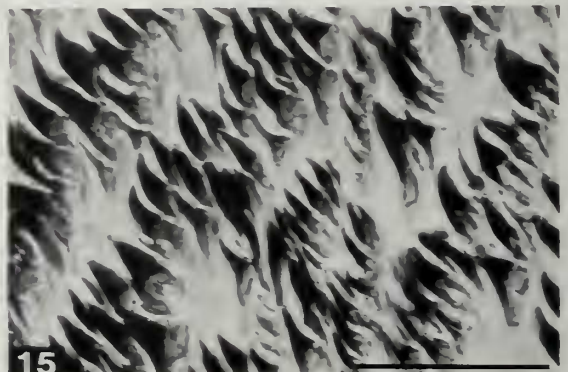
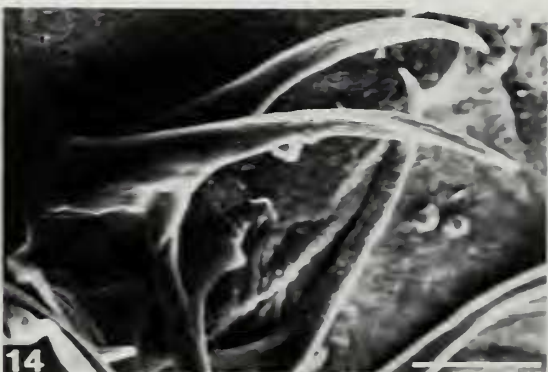
Figure 5. Entire left jaw laid flat showing inner surface.

Figure 6. Mandibular elements from inner face of jaw: a, mid-central group from posterior end of jaw; b, marginal group from anterior end; c and d, mid-central groups from anterior end.

Figure 7. Prostate gland as dissected off bursa copulatrix and laid flat; view of inner surface.

Figure 8. Detail of distal section of vas deferens and penis. Abbreviations: d.v.d., distal vas deferens; p., penis; p.s., penial sac; p.sh., penial sheath.

Figure 9. Diagrammatic view of structure of reproductive organs of a mature adult (ovotestis, nidamental glands, and penial sac not shown). Abbreviations: amp., ampular region of hermaphrodite duct; b.c., bursa copulatrix; p., penis; pr., prostate gland; p.sh., penial sheath; r.s., receptaculum seminis; v., vagina.



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Explanation of Figures 10 to 17

Figures 10 to 17. Radula and jaws of *Bathyberthella antarctica*.

Figure 10. SEM of inner lateral radular teeth. Bar = 100 μm .

Figure 11. SEM showing detail of cusps of several middle lateral teeth. Bar = 20 μm .

Figure 12. SEM of outermost lateral teeth from two radular rows. Bar = 100 μm .

Figure 13. SEM of group of middle lateral teeth from center of radular row. Bar = 100 μm .

Figure 14. Detail of isolated middle lateral teeth. Bar = 40 μm .

Figure 15. Photomicrograph of mandibular elements from inner face of jaw; marginal group from anterior end of jaw. Bar = 25 μm .

Figure 16. Photomicrograph of mandibular elements from inner face of jaw; mid-central group from anterior end of jaw. Bar = 25 μm .

Figure 17. Photomicrograph of mandibular elements from same region of jaw as Figure 16. Note fine subdenticles flanking cusps. Bar = 25 μm .

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